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PODAGRITUS CORA (CAMERON) AND *P. ALBIPES* (F. SMITH) (HYMENOPTERA: SPHECIDAE: CRABRONINAE) PREYING ON EPHEMEROPTERA AND TRICHOPTERA

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Abstract.—*Podagritus albipes* (F. Smith) and *P. cora* (Cameron) are recorded preying almost exclusively on a *Deleatidium* sp. taxonomically close to *D. myzobranchia* Phillips, a *Deleatidium* sp. close to *D. lillii* Eaton (Ephemeroptera) and *Pycnocentrodes aureola* (McLachlan) (Trichoptera). Multitudes of individuals of these carbronines, together with predatory muscids (*Spilogona* Schnabl), occupy large stones in the Blue Stream (Mt. Cook National Park, New Zealand) that protrude above waterlevel. When Ephemeroptera nymphs eclose as subimagines and emerge from the water onto the stones, they are often captured either by *Podagritus* wasps or by *Spilogona* muscids. The wasps take the prey to nests in patches of sand on either side of the stream. Forty (of 41) excavated *Podagritus* nests contained only Ephemeroptera and Trichoptera. This association reoccurs every summer. The *Podagritus* populations generally do not feed upon the Diptera, prey usually associated with this genus.

Key Words.—Insecta, Sphecidae, *Podagritus cora, Podagritus albipes,* Diptera, *Spilogona,* Ephemeroptera, *Deleatidium,* Trichoptera, *Pycnocentrodes aureola*

Podagritus Spinola comprises 53 described species distributed in South America (28), Australia (19) and New Zealand (6); New Zealand has an additional two undescribed species. Species of this genus provision their nest cells exclusively with Diptera (Bohart & Menke 1976). The present observation is unusual because it shows that nesting aggregates along the entire course of a stream prey almost entirely on aquatic insects, mostly Ephemeroptera and Trichoptera. The vast majority of provisioned nest cells in this locality were completely devoid of Diptera.

A brook, the Blue Stream, originates from Tasman Glacier, Mt. Cook National Park, New Zealand, emerging from the southern side approximately 8500 m upstream of the terminal face of the glacier. Blue Stream runs for approximately 2 km along the southern wall of the Tasman Valley before joining the Tasman River. The stream flows over outwash plains of boulders, gravel, shingle and sand; large stones line its course and many boulders protrude above the surface of the water.

OBSERVATIONS

There are large numbers of Ephemeroptera (principally *Deleatidium myzobranchia*-group, *D. lillii*-group) and Trichoptera (*Pycnocentrodes aureola* [McLachlan]), besides lesser numbers of miscellaneous immature aquatic insects on the undersurfaces of the stones. During November–February between 11:00–16:00 h, ultimate instar mayfly nymphs crawl rapidly from the undersides of boulders, and emerge from the water. They stop (about 2 min after first appearing underwater on the stone) and eclose to a subimago, that is free in 2–8 min. Teneral caddisflies also emerge along the sides of the stones, pausing above the water

level. Large numbers of crabronine wasps, mostly *Podagritus cora* (Cameron) and *P. albipes* (F. Smith), together with an undescribed muscid fly (*Spilogona* Schnabl, formerly *Limnophora* Robineau-Desvoidy) are also on the stones. In January there are up to 24 crabronines and five muscids per boulder, but more usually there are two to six crabronines and two muscids per stone. On warm sunny days between mid October and February, every available stone in the stream may be occupied thusly, and the flies and wasps wait for mayflies and caddisflies. The predators frequently observe the submerged prey and move closer to their emergence points. During the peak emergence of mayflies (often 13:00–15:00 h) crabronines fly from the tops of the boulders to the eclosing mayfly nymphs (Fig. 1) and, as the integument splits, pull the subimago out, sting and paralyze it, and fly rapidly about 15 m to sand patches on the sides of the stream where they nest. Most of the nest-cells throughout a 1.5 km area on both sides of the Blue Stream are provisioned solely with mayflies, although about 10% of nests contain a combination of mayflies and caddisflies.

The muscids are capable of defending their prey against relatively large crabronines such as *P. cora* with which they compete for mayflies (Fig. 2), despite that in other parts of the country this wasp frequently provisions its nests with large sarcophagids and calliphorids. Examination of 40 crabronid nests at the Blue Stream indicated that *Spilogona* were not used as prey; no sphecids were observed to take *Spilogona.*

On overcast days when the crabronines remained underground in their burrows the muscids were present on the boulders; the flies were also present on the boulders for longer periods during sunny weather, arriving earlier and leaving later than the wasps. They frequently captured and consumed aquatic insects on the boulders.

The crabronines were best able to capture emerging mayflies on still, warm, sunny days. When a small wind developed, the wasp and its prey were frequently blown into the stream and swept away with the current. Mayfly subimagines frequently fell into the stream by themselves and drifted away; some of these, however, were plucked from the surface of the water by crabronines, stung in mid-air, and transported to the nests.

Both *P. cora* and *P. albipes* would attempt to take struggling insects held by the surface tension of the water, but neither would accept as prey anything other than *Deleatidium* subimagines or *Pycnocentrodes aureola.* On six occasions, *P. albipes* females flew to a struggling *Syrphus novozealandiae* (Diptera: Syrphidae), a provisioned prey in its nests elsewhere, but these flies were ignored once identified by the wasps at Blue Stream.

The association between *Podagritus, Spilogona, Deleatidium* and *Pycnocentrodes* species at Blue Stream has occurred every summer since at least 1975, beginning in November and ending at the end of February.

Although the *Deleatidium* ultimate instar nymphs taken by *Podagritus* wasps at Blue Stream key to the *myzobranchia*-group and the *lillii*-group using Winterbourne et al. (1981), and the subimagines key to *D. myzobranchia* Phillips and *D. lillii* Eaton using Phillips (1930), the two species taken from crabronine wasps are both undescribed (M. Winterbourne, personal communication).

Nests.—Podagritus albipes nests were made in level sand. The 3.0 mm wide entrance typically opened in the middle of a 40 mm diameter mound and was left open during provisioning. The 3 mm wide main burrow sloped at 75°–77°

Figures 1, 2. Figure 1. Three *Podagritus cora* females competing for a *Deleatidium* sp. subimago (undescribed), that is emerging from its nymphal exuviae. One *P. cora* has grasped the subimago, pulling it out. Other mayfly exuviae are visible. Figure 2. A *Spilogona* sp. (undescribed) has beaten a *Podagritus cora* to a *Deleatidium* sp. subimago (undescribed) that started emerging from its last nymphal exuviae.

and the first cell was 10–68 mm (typically 60 mm) below surface level. Nests contained either one or two cells. The cells contained four to six mayflies (*Deleatidium myzobranchia*-group, *D. lillii*-group), and less frequently a combination of mayflies and caddisflies (*Pycnocentrodes aureola*). Of 15 nests excavated, 11

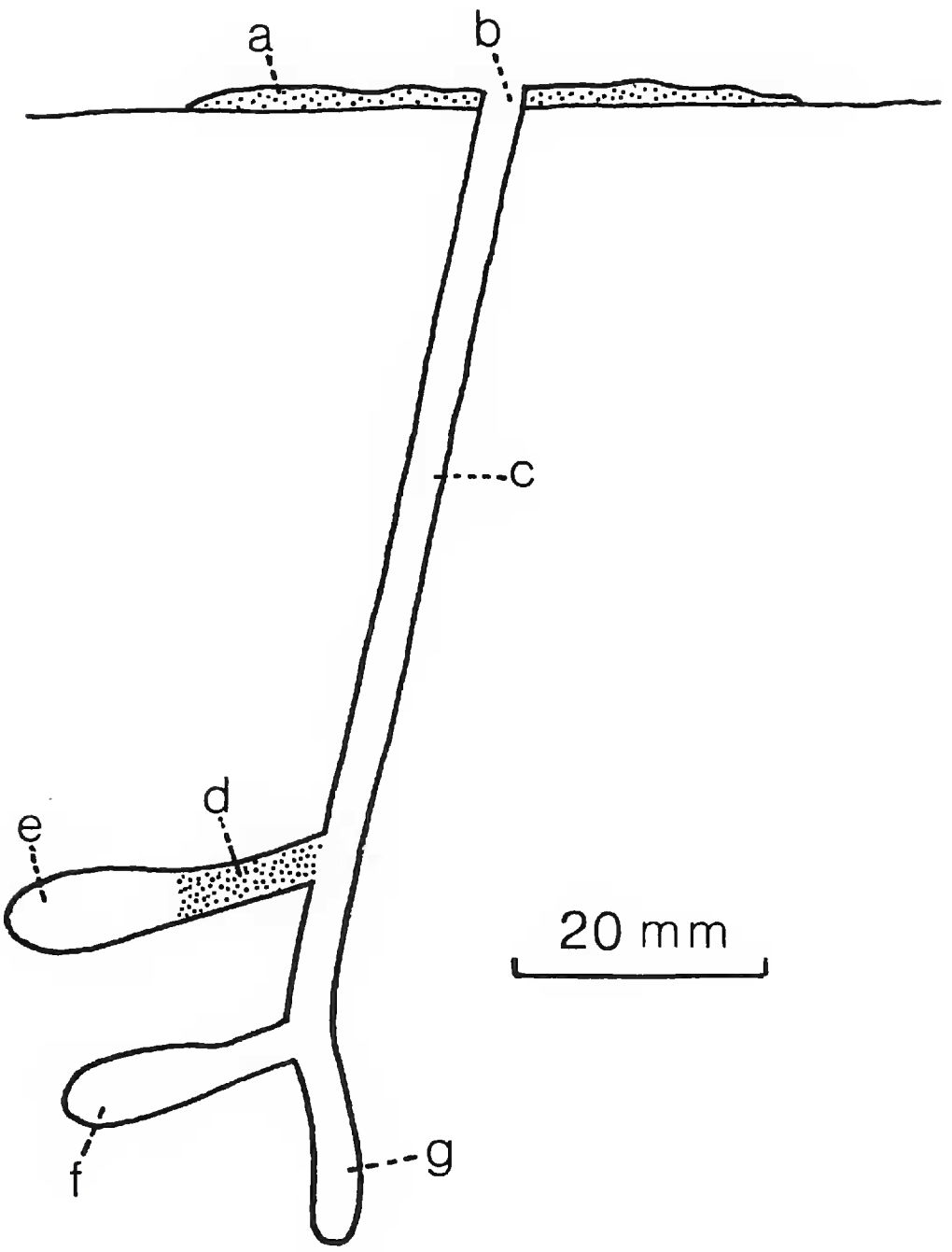

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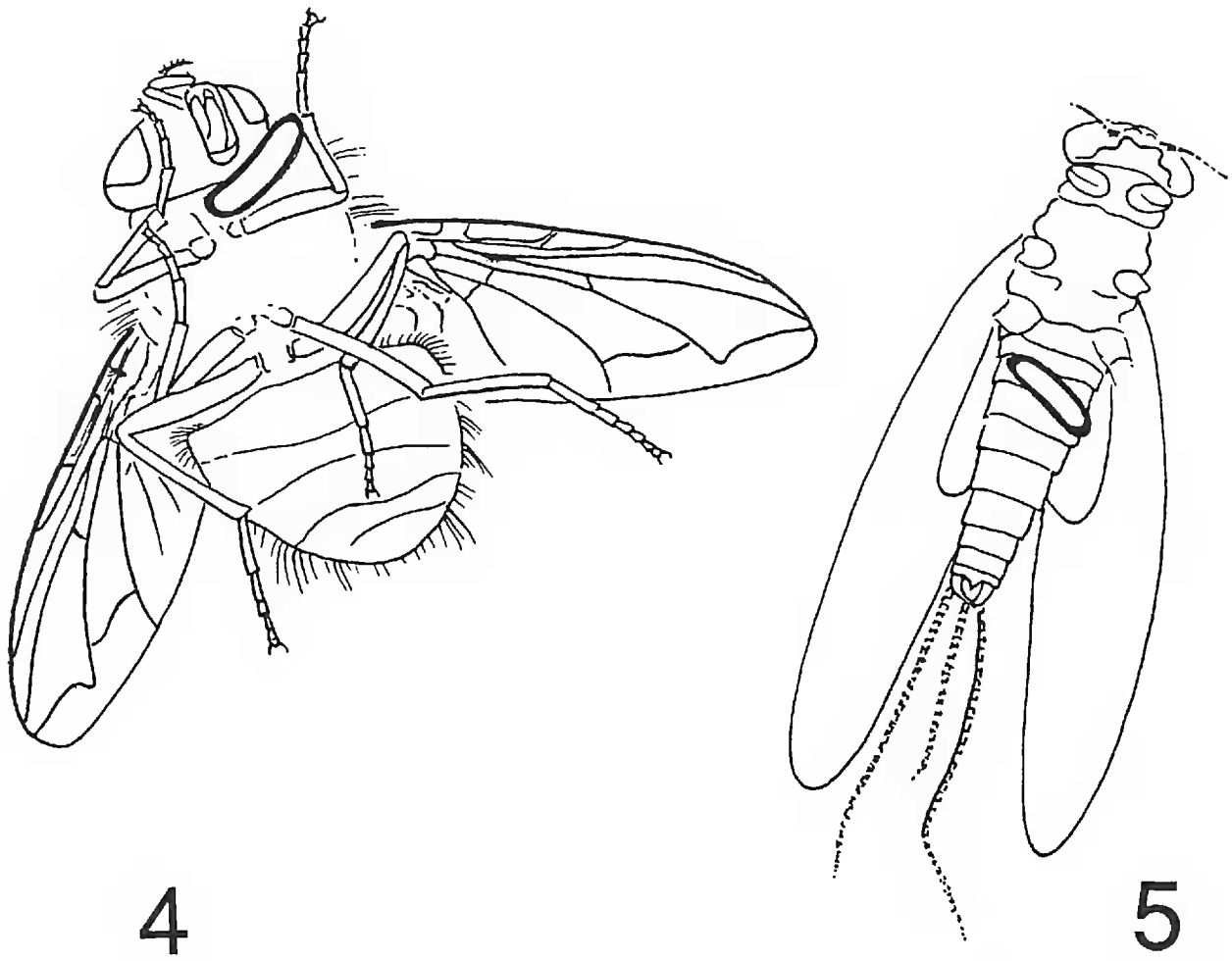
Figure 3. Typical nest of *Podagritus cora* at Blue Stream. a. Mound. b. Entrance. c. Main burrow. d. Inner closure. e. Provisioned cell. f. Partly provisioned cell. g. Spur.

were one-celled and four were two-celled. Total prey comprised *Deleatidium myzobranchia*-group and *D. lillii*-group (n = 89) and *Pycnocentrodes aureola* (n = 22). All prey were positioned supine (venter up) facing the ends of the cells. After an egg was laid on the prey, the cell-burrow, but not the main burrow was closed.

Podagritus cora nests were made in level sand. The entrance was a 3.5–3.9 mm wide round hole in the center of a 30–50 mm wide mound. Nests were sometimes dug beside stones. The main burrow was 3.5–3.9 mm wide and the first cell was 65–80 mm below the surface. The cells were on average 4.6 mm wide (greatest diameter) and 9.2 mm long. Fifteen nests were excavated, and of these nine were single-celled and six had two cells. Total prey comprised 139 *Deleatidium my-*



Figures 4, 5. Figure 4. Position of egg of *Podagritus cora* on *Calliphora quadrimaculata*. Figure 5. Position of egg of *P. albipes* on *Deleatidium* sp. subimago (Blue Stream). When preying on Diptera in other areas, eggs are positioned in the neck region, as in Fig. 4. (Both figures are tracings from photographs.)

zobranchia-group and *D. lillii*-group and 23 *Pycnocentrodes aureola*. The cells contained seven to eight mayflies or eight mayflies and one caddisfly. Eggs laid on mayflies were usually placed on the third and fourth abdominal sterna (Fig. 5). These same species place eggs on the neck region when utilizing Diptera as hosts. All prey were placed in the cells supine with the head facing the end of the cell. Main burrows were left open during provisioning.

Both *P. albipes* and *P. cora* held the mayfly upside-down, grasped by the mesothoracic legs, with the wings of the caddisfly projecting. The wasp would descend slowly towards the nest and fly directly in without alighting on the sand.

On 24 Jan 1989 a solitary *P. cora* (initally assumed to be *P. swalei* until captured) spent much time at the entrance to a rabbit burrow, preying on large flies. Its nest was made in the sand, beside the burrows of its peers, and was single-celled. The nest contained two *Calliphora quadrimaculata* (Swederus) and one undetermined sarcophagid of similar size. The egg was placed between the head and thorax of the fly.

The nests of *Podagritus* species were invaded by larvae of an undescribed *Anabarynchus* (Diptera: Therevidae) which burrowed through the sand and devoured the provisioned food as well as the developing immature wasps. The adult stage of this therevid had a slate-grey body and white, black-veined wings; it frequents the sandy patches during summer.

Discussion

Throughout its range in the Southern Hemisphere, *Podagritus* has been recorded as preying only on Diptera (Bohart & Menke 1976). Solitary wasps capture prey in habitats different than and often distant from their parental nest or where they eventually build their own nests (Evans 1966, Evans & Eberhard 1970). Therefore, the wasp must undertake initial hunting flights involving random flight before it locates a source of appropriate prey. Sphecid wasps apparently learn certain sources of prey, and return to them until the source is exhausted; they do not normally make mistakes with respect to prey.

New Zealand *Podagritus* prey mostly on Diptera, but frequently take other insects occasionally. *Podagritus albipes* and *P. cora* stock their nest-cells with a combination of Diptera and Ephemeroptera from streams in the Tararua Range, the South Island West Coast, and elsewhere (unpublished data), and *P. albipes* uses predominantly Diptera but also Ephemeroptera at the Hutt River (D. Willis, personal communication). *Podagritus parrotti* frequently stocks its nests with small beetles (*Cyphon* spp. [Scirtidae], *Asilis tumidus* Broun [Cantharidae], *Luperus vulgaris* Broun [Chrysomelidae]) captured from flowering shrubs (unpublished data; J. Charles, personal communication). Notwithstanding this evidence, such instances usually appear almost as exceptions to the rule that *Podagritus* in New Zealand are specialists on Diptera.

Despite such frequent break-downs in prey specificity among New Zealand *Podagritus,* the situation at the Blue Stream is unusual. Throughout almost the entire length of the Blue Stream, *P. albipes* and *P. cora* prey almost exclusively on mayflies and, to a lesser extent, caddisflies and appear to reject seemingly more appropriate prey. On six occasions, after careful examination, *P. cora* and *P. albipes* females rejected syrphid flies (their usual prey). The association with mayflies and caddisflies probably represents a population in evolutionary transition, as noted in Australia involving the widespread genus *Bembix* Fabr. (Evans & Matthews 1973). *Bembix* is best represented in North America, where Evans & Matthews (1973) suggest that *Bembix* evolved, and later spread to other regions. Evans accumulated thousands of prey records for *Bembix* in North America, without finding a single record outside Diptera (Evans & Matthews 1973). *Bembix* is also well represented in Australia, and Evans & Matthews (1973) found 14 species that preyed exclusively on Diptera, one which preyed on both flies and damselflies (Odonata: Anisoptera), one that preyed on both flies and wasps, and six that were each host specific for Hymenoptera, Odonata and Neuroptera. They regarded the former as "species in transition," and assumed that the six Australian *Bembix* species that prey on single orders of insects exclusive of Diptera passed through similar transitional stages. Wheeler & Dow (1933) suggested that if the (then unidentified) *Bembix* that Wheeler observed capturing damselflies in Australia was taking its normal prey, it represented a "comparatively recent development in evolution."

The situation at Blue Stream seems similar and may indicate how sphecids which characteristically exhibit host specificity at the ordinal level change their host preference to entirely new orders. Alternatively, the New Zealand *Podagritus* might not be specialist hunters of Diptera, but rather prey generally on Diptera, taking other orders if a good source of prey is located.

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